

Predicting autumn phenology: How deciduous tree species respond to weather stressors

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ABSTRACT

Shifts in the timing of autumnal leaf coloration and leaf drop in temperate forests with climate change can have substantial impacts on community and ecosystem processes (e.g. altered carbon/nitrogen cycling and biotic interactions). However, the environmental control of autumn phenology remains significantly understudied in striking contrast to spring phenology. In this study, we used linear mixed effects model with ground-based phenology observations in northeastern USA and found that both weather stressors (e.g. heat- and drought-stress and heavy rainfall) during the growing season and spring phenology significantly affected inter-annual variation in autumn phenology of twelve dominant deciduous tree species. While warm temperatures and drought lead to later fall phenology for most species, heavy rainfall and heat stress lead to earlier leaf coloration and leaf drop. We also found that the phenological sensitivities to weather stressors are diversely species-specific. Under future climate change projections, we predicted that greater summer heat-stress in the future will cause abbreviated leaf coloration seasons for most species. Our mixed-effects modeling framework suggested that accounting for phenological variations among individual trees, species and sites largely improved model predictions, which should not be overlooked in phenological model development. Our study improves our understanding of how species-specific autumnal phenology responds to weather stresses, and describes a new modeling framework to investigate both inter-annual phenological changes and local variations among trees, species, and sites. Our predictions on autumn phenological shifts will help in assessing the effects of climate change on forest community and ecosystem processes in the future.

1. Introduction

Climate change to date has caused dramatic plant phenological shifts in both spring and autumn in temperate regions around the world (Doi and Takahashi, 2008; Körner and Basler, 2010; Polgar and Primack, 2011; Jeong et al., 2011; Visser, 2016), which can in turn influence ecological processes substantially, including C and N cycling, hydrology, demography, and biotic interactions (Vitasse et al., 2009; Fridley, 2012; Pépino et al., 2013; Estiarte and Peñuelas, 2015; Thackeray et al., 2016; Elmore et al., 2016). For example, delays in autumn phenology (i.e. timing of leaf coloration and leaf drop) that lead to extended growing seasons, may increase the risk of freezing damage from early autumnal frosts, preventing reabsorption of nutrients from leaves and altering nutrient cycles (Niinemets, 2010; Norby et al., 2003; Richardson et al., 2013). Changes in the phenology of foliage coloring may alter cues for animal behaviors such as avian migration (Ellwood et al., 2015). The timing of fall foliage color change

also impacts the multi-billion dollar fall foliage ecotourism industry, especially in the northeastern United States (Rustad et al., 2012; Spencer and Holecek, 2007). However, the autumn phenological responses in plants to environmental changes remain poorly understood (Gallinat et al., 2015). The important key environmental factors that affect plant autumn phenology and the species-specific responses thereto, other than frost or chill-stress, remain largely unknown.

Our knowledge of the environmental control of leaf senescence in temperate deciduous woody plants has changed surprisingly little over the past 60 years (Lim et al., 2007; Samish, 1954). In the 2007 review by Lim and colleagues (Lim et al., 2007), the factors that most likely affect the timing of leaf coloration and drop in the autumn were suggested to include day length, heat, cold, drought, wetness, nutrient and pathogen attack. But previous studies of environmental influences on autumn phenology have focused only on the effects of autumn chilling, frost, and/or day length (Archetti et al., 2013; Delpierre et al., 2009; Gill et al., 2015; Jeong and Medvigy, 2014); one exception is the study

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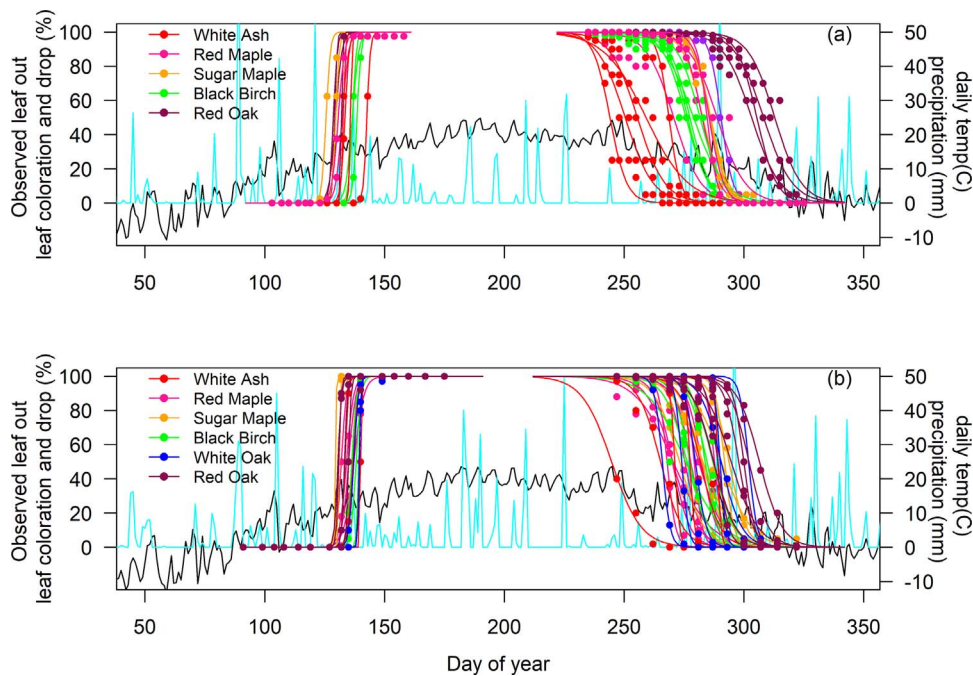


Fig. 1. Observed leaf phenology of 6 common deciduous tree species in spring and autumn in 2014 at the RMP site in UCONN Forest (a) and at Harvard Forest (b). Each color indicates one species. Each dot is one observation. Each curve line is a logistic curve fitted to the observations. Daily temperatures ($^{\circ}\text{C}$) and precipitation (mm) are shown as black and light blue lines respectively. Spring phenology shows leaf unfolding, and autumn phenology includes leaf coloration and leaf drop. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

considering the effects from precipitation (Estrella and Menzel, 2006), and our own study of fall phenology based on satellite-derived data (Xie et al., 2015b). Although physiological experiments have reported the effects of a subset of these factors (i.e. temperature, day length, and drought) on plant leaf coloration and leaf drop (Fracheboud et al., 2009; Naschitz et al., 2014; Rosenthal and Camm, 1997), few studies have identified the relative importance of contributing factors or quantified their effects (Estrella and Menzel, 2006). Our previous study found that other than decreasing temperature in autumn, moisture conditions and extreme weather events across the entire growing season (e.g. drought, heat stress and heavy rainfall) all have significant effects on the timing of autumn senescence at the forested landscape scale (Xie et al., 2015b). However, it is unclear how autumn phenology of temperate forest tree species responded individually to these environmental stresses. Since forest tree species with various physiological structures and mechanisms showed different strategies in response to environmental changes (Diez et al., 2012; Tang et al., 2016), we expect diverse sensitivities to stressors in autumn phenology among forest tree species. While temperate forest communities may change species compositions spatially, understanding species-specific autumn phenology responses to potential environmental stressors is critical to assessing phenological shifts and impacts for the forest communities at regional and landscape scales (Richardson et al., 2013; Jeong and Medvigy, 2014).

Diverse phenological responses among plant species were widely recognized by previous studies (Estrella and Menzel, 2006; Primack et al., 2009; Vitasse et al., 2009). However, variations in phenology among individuals or locations within tree species are often overlooked in phenological modeling, even though they have been noted (Crawley and Akhteruzzaman, 1988; Ne'Eman, 1993; Delpierre et al., 2017). The risk of ignoring phenological variation among individuals and locations that may be associated with ontogeny or sites effects, could result in overestimates or underestimates of phenological variation driven by diverse environmental factors, which in turn will lead to biased predictions of phenological responses to environmental changes. Thus, instead of treating phenology of each individual or at each location as independent of each other, we expect the new modeling framework developed here not only to explain species-specific autumn phenological responses to the important climate/weather factors, but also to include the variation in phenology due to site and individual effects.

In addition, positive relationships between spring and autumn phenology were reported (Fu et al., 2014; Keenan and Richardson, 2015), which indicates a more complex mechanism of phenological responses of plants and points to our general lack of understanding of the phenological activities of plants across the entire growing season. Since both spring and autumn phenologies of plants are likely responding to climate change, the influences of phenological changes in the spring should also be included in building models to explain phenological changes in autumn in response to climate change.

Our study focuses on autumn phenology from the beginning of leaf coloration through the end of leaf drop for 12 dominant deciduous tree species of northeastern United States forest communities. The objectives are: 1) to identify important climatic and weather factors affecting autumn phenology of deciduous tree species; 2) to quantify species-specific phenological responses to the important environmental factors; 3) to develop a modeling framework to explain phenological variation inter-annually and among trees, species and sites; and 4) to predict future autumn phenological shifts of deciduous tree species driven by projected climate change.

2. Methods

2.1. Phenology and climate data

We used two sets of phenology ground observations in this study. One is from five sites in Connecticut USA (2012–2014), and the other is from Harvard Forest (1993–2014) (Fig. 1 and Table S2). To collect phenology data in Connecticut, we established 5 plots (25m $\times$ 50m) that stratified local site conditions (i.e. variation in soil and soil moisture and species composition) in the natural forest landscapes in and around the University of Connecticut (UCONN) campus. We randomly selected 88 individuals of eight dominant tree species differentially present in five sites (Table S2). The eight species were: red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), black birch (*Betula lenta*), pignut hickory (*Carya glabra*), shagbark hickory (*Carya ovata*), white ash (*Fraxinus americana*), white oak (*Quercus alba*), and red oak (*Quercus rubra*). In total 88 individual adult trees were observed from 2012 to 2014. We observed leaf phenology for each individual, including bud burst, leaf unfolding, leaf coloration and leaf drop (cf. Figs. 1 and S1). Observations were conducted twice a week (Table S1)

in spring from late April when buds began to break to early June with full leaf out and in autumn from late August with initial leaf coloration to middle November ending with leaf drop (see observation protocol in Supplementary Materials). Hourly temperatures were recorded by temperature probe loggers at each plot. Daily precipitation data was available from the weather station in Storrs, Connecticut, USA, from the United States Historical Climatology Network (USHCN) (<http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html>).

Long term phenology observation on 12 deciduous tree species (52 individual trees) and daily weather data (daily mean, maximum, and minimum temperatures, and precipitation) at Harvard Forest (<http://harvardforest.fas.harvard.edu/data-archives>) from 1993 to 2014 were used to provide a long-term observation dataset to complement the data we collected in Connecticut. The twelve species at Harvard Forest were: striped maple (*A. pensylvanicum*), red maple (*A. rubrum*), sugar maple (*A. saccharum*), yellow birch (*B. alleghaniensis*), black birch (*B. lenta*), paper birch (*B. papyrifera*), grey birch (*B. populifolia*), American beech (*Fagus grandifolia*), white ash (*F. Americana*), white oak (*Q. alba*), red oak (*Q. rubra*), and black oak (*Q. velutina*) (Table S2). Harvard Forest phenology observations used a very similar protocol (<http://harvardforest.fas.harvard.edu>) to that which we used in Connecticut (see Supplementary Materials). The phenophases we used in this study included bud break, leaf coloration and leaf drop. Since bud break in the Harvard Forest observation protocol (buds on the tree that have broken open revealing leaves) and leaf unfolding in UCONN observation protocol (one or more live unfolded leaves are visible) indicate closely similar plant life events, we used leaf unfolding events for both.

The percentage of the canopy in each of three phenophases (i.e. leaf unfolding, leaf coloration and leaf drop) was visually estimated (Table S1). We fitted logistic curves to the observational data (Figs. 1, S1) to estimate three phenological transition dates (onset, peak and end date) for each individual tree. Onset and end dates of each phenophase were determined by points at where there was minimum change of curvature. They indicated the beginning and the end of the phenophases. The peak date was determined by the inflection point of fitted logistic curves, which was the timing when leaf unfolding, leaf coloration and leaf drop changed most quickly.

Multiple derived weather variables (Table S3) were developed from daily temperature (measured at each of our sites) and precipitation records (from the Storrs weather station) to explain the change in phenological transition dates spatially and temporally. We first built a list of weather variables for potential environmental conditions that may affect fall phenology including: cold-stress, frost, heat-stress, rainfall, drought-stress, and flooding events (Table S3) (Xie et al., 2015b). Previous studies have considered accumulating cold degree days (CDD) and decreasing day length that occur in fall as the primary triggers of leaf coloration and leaf drop (Archetti et al., 2013; Jeong and Medvigy, 2014; Richardson et al., 2006). Considering the important effects from minimum temperature or chilling-stress on autumn phenology (Kalcisits et al., 2009; Tanino et al., 2010), we developed a comparable index CDDi using minimum temperature as base temperature (Table S3) to measure chilling based on night temperatures in the autumn. We did not investigate the effect of day length effect since day length does not have year-to-year variation among individuals within sites, and due to the very small differences in day length between UCONN and Harvard Forest which has a negligible effect relative to other variables, but are accounted for as site random variable effects. We also developed other climate/weather variables in Table S3 to represent environmental stressors potentially affecting tree performance (Duque et al., 2013; Niinemets, 2010). Plant phenological responses to stresses may differ depending on when stresses occur in different seasons (Bréda et al., 2006). The physiological requirements regarding thermal and moisture conditions that trigger tree developmental stages may also differ in different phenophases as well as among tree species (Primack et al., 2009; Wilczek et al., 2010; Hwang et al., 2014). Three sets of weather variables were calculated: growing season drought-

stress (GDR), rainy days (RD), and heavy rainy days (ECA), for three periods that reference spring, summer and autumn intervals (i.e. May.1–Jun.30, Jul.1–Aug.31, and Sep.1–Oct. 30, respectively). For our index of cold degree days (CDD and CDDi), we examined the effects of different base temperatures (daily minimum and mean temperature at 10°, 15°, and 20 °C) for three months (August, September and October) to determine which monthly period of CDD, with what base temperature, may best explain autumn phenology variation among the deciduous tree species. We used 35 °C as the threshold temperatures for hot days (HD) indicating heat-stress, and we found HDs only occurred in July and August at the study sites. We calculated frost days (FD) in two months (September and October) indexing a cold-stress that differs from chill-stress: CDD.

We obtained downscaled climate projection data for one global climate model (GCM, GFDL-ESM2G) with one future scenarios (RCP 8.5) from Multivariate Adaptive Constructed Analogs group for model predictions (Abatzoglou and Brown, 2012). The GCM was selected based on the relatively good performances in the estimation of North America climate and hydrological variables and extremes for the continent (Sheffield et al., 2013). We used daily maximum and minimum temperature and daily precipitation at the location of Harvard Forest to calculate climate/weather variables for future predictions from 2015 to 2099.

2.2. Statistical modeling

We used linear mixed effects models to explain the relationships between autumnal phenology and climatic variables for different species and sites. Linear mixed effects models consider heterogeneity and dependence from nested data structure with repeated measurements on individuals and sites. The advantages of linear mixed effect models are that they allow incorporation of random effects due to variation in phenology among individuals (Fig. S2), species and sites levels, while estimating the effects from climate/weather variables on leaf phenology.

We fitted linear mixed effects models using two datasets. One is the dataset including observations on eight species from both UCONN and Harvard Forest during 2012 and 2014. Six phenological transition dates (3 of leaf coloration and 3 of leaf drop – cf. Fig. S1) were separately fitted as response variables in the models. Random intercept models with species and sites as random effects were used in the dataset. Potential climate/weather factors and spring phenology were set as fixed effects in the model. Important factors (variables) were identified for each transition dates of leaf coloration and leaf drop using Akaike Information Criterion (AIC) (Akaike, 1998) and Bayesian Information Criterion (BIC) (Schwarz, 1978) as selection criteria. Smaller AIC and BIC values indicate better model fit. BIC has a larger penalty term than AIC that favors smaller number of parameters in the model. While inter-annual variation in phenology were explained by climate/weather factors, variation in phenology among species and sites were indicated by random intercepts; this yields a mixed-effects model with two hierarchical levels: species and site effects. One climatic factor with the highest contribution to explaining the response variables was selected from multiple climatic factors with high correlation ($r > 0.5$) to avoid multicollinearity in the model. The top five best models were reported for each phenological transition date.

The 3-year (2012–2014) phenology dataset, and the two-level mixed-effect model used to analyze it, were sufficient to reveal phenological variation among multiple sites, but was insufficient to identify differences in the sensitivity to climatic factors among species, or to incorporate individual phenological variation within species. This was because the sample size of the 3-year dataset was not large enough to support a complex mixed-effects model structure with an added hierarchy of phenological variation at the individual level and random slopes at the species level. Thus, we used the long-term dataset from Harvard Forest from 1993 to 2014 as the *second dataset* to fit random

intercept and slope models with species and individuals as random effects. This long-term phenology dataset allowed the models to focus on phenological variation among individuals and species at one site. This is still a two-level hierarchical model structure, but with a different focus: resolving differences in phenology among species and individuals within species, versus among species and sites. This second dataset included 933 observations on 12 species (52 individuals) over 22 years. We randomly selected 10% of the data (93 observations) as the validation data and used 90% (840 observations) as the model training data. Climate/weather factors and spring phenology were used as fixed effects, and species and individuals were random effects in the model. Random slopes at the species level explain species-specific phenological responses or sensitivities in autumn to changes in climate/weather factors.

We used a top-down strategy (Diggle, 2002; West et al., 2015; Zuur et al., 2009) to build models and selected the best models using marginal AIC (mAIC) for fixed effects and conditional AIC (cAIC) for random effects (Greven and Kneib, 2010) (see model selection procedures in Supplementary Materials). Data were analyzed using R software (R Core Team, 2015) with R packages ‘nlme’ (Pinheiro et al., 2014), ‘lme4’ (Bates et al., 2015), p. 4) and ‘cAIC4’ (Saeften and Ruegamer, 2014), p. 4). Best models were reported for six phenological transition dates (3 for leaf coloration and 3 for leaf drop cf. Fig. S1). Using the best models identified by the above criteria we predicted six phenological transition dates for 93 observations in Harvard Forest across 12 species and 21 years. We compared predicted dates to the observed phenology dates and calculated r^2 and root mean square error (RMSE) to show the goodness of model fit for model evaluation.

Future predictions for autumn phenology of deciduous trees at Harvard Forest were based on future climate change and spring phenological changes. Linear mixed effect models were also applied to estimate spring leaf unfolding dates (i.e. onset, peak and end dates) of 52 individual trees at Harvard Forest (1993–2014). Monthly mean temperature in March, April and May, cumulative growing degree day (GDD) and chilling units (CU) from January 1st to May 31st were used as fixed variables (Xie et al., 2015a), while species and individual trees were random effects in the models. Random slopes at the species level explain species-specific phenological responses in the spring to changes in these climate/weather factors. Best models for phenological dates were selected following the same procedure as for fall phenology (see model selection procedures in Supplementary Materials) and were used to predict spring phenological changes in future years in response to projected climate change (2015–2099) at the individual level. Then we used predicted spring phenological changes and future climate projection data to predict autumn phenology for future years for each individual tree (2015–2099).

3. Results

3.1. Important factors affecting autumn phenology

For three phenological transition dates of leaf coloration of eight common tree species from multiple sites (i.e. dataset 1: five sites at Connecticut and one site at Harvard Forest) during 2012 and 2014, the best model showed that chilling based on minimum temperature (CDDi) in August or September, and summer rainfall (RD_(Jul.1–Aug.31)) are important factors affecting the timing of leaf coloration processes (Table 1). In contrast, for onset, peak and end dates of leaf drop, only chilling in either just October or over three months (August, September, and October), based on minimum temperature at 10 °C (CDDi_{Oct10} or CDDi_{ASO10}), had significant effects on the timing of the leaf drop processes (Table 1); this points to the important effect from night temperatures on plant growth cessation and bud set (Kalcits et al., 2009; Tanino et al., 2010). However, the small difference in AIC and BIC among the five best models indicated the potential importance that drought-stress and precipitation, in addition to chilling in autumn, may

Table 1

Best five mixed-effects models for each phenophase of autumn phenology for 8 species in Connecticut and Harvard Forest from 2012 to 2014. Random effects include intercepts for both species and site levels. Variables included in the models are all statistically significant. Bold numbers are smallest AIC and BIC. For variables names refer to Table S3. CDD: cold degree day; RD: rainy day; ECA: heavy rainy day; GDR: growing season drought; FD: frost day; T_{min}: monthly minimum temperature. Subscript in each variable indicates the time period for each variable or the base temperature in calculations. LUs is leaf unfolding onset date, and LUp is leaf unfolding peak date.

Phenological transition date	Fixed effects in models	AIC	BIC
Leaf coloration onset date	CDDi _{Aug10} + RD _(Jul.1–Aug.31) + LUs	2192.1	2218.3
	CDDi _{Aug10} + ECA _(Sep.1–Oct.31) + LUs	2195.4	2221.5
	CDDi _{Aug10} + GDR _(Sep.1–Oct.31) + LUs	2202.9	2229.0
	FD _(Sep.1–Oct.31) + GDR _(Sep.1–Oct.31) + LUs	2203.4	2229.5
	CDDi _{Aug10} + RD _(Sep.1–Oct.31) + LUs	2205.5	2231.6
Leaf coloration peak date	CDDi _{Aug10} + RD _(Jul.1–Aug.31) + LUs	2109.6	2135.7
	CDDi _{Aug10} + ECA _(Sep.1–Oct.31) + LUs	2113.9	2140.1
	FD _(Sep.1–Oct.31) + RD _(Jul.1–Aug.31) + LUs	2114.4	2140.5
	CDDi _{Aug10} + GDR _(Sep.1–Oct.31) + LUs	2118.6	2144.7
	CDDi _{Aug10} + RD _(Sep.1–Oct.31) + LUs	2120.8	2146.8
Leaf coloration end date	CDDi _{Aug10} + RD _(Jul.1–Aug.31) + LUp	2105.1	2131.2
	CDDi _{Aug10} + ECA _(Sep.1–Oct.31) + LUp	2106.5	2132.6
	FD _(Sep.1–Nov.31) + RD _(Jul.1–Aug.31) + LUp	2106.8	2132.9
	CDDi _{Sep10} + GDR _(Sep.1–Oct.31) + LUp	2108.3	2134.4
	CDDi _{Sep10} + RD _(Sep.1–Oct.31) + LUp	2109.6	2135.6
Leaf drop onset date	CDDi _{Oct10} + LUs	2132.3	2154.6
	CDDi _{ASO10} + LUs	2132.8	2155.2
	T _{min-Oct} + LUs	2133.9	2156.3
	RD _(Sep.1–Oct.31) + LUs	2135.8	2158.1
	GDR _(Sep.1–Oct.31) + LUs	2136.9	2159.2
Leaf drop peak date	CDDi _{Oct10} + LUs	2075.1	2097.5
	CDDi _{ASO10} + LUs	2075.2	2097.6
	T _{min-Oct} + LUs	2076.0	2098.4
	RD _(Sep.1–Oct.31) + LUs	2080.0	2102.4
	GDR _(Sep.1–Oct.31) + LUs	2081.7	2104.1
Leaf drop end date	CDDi _{ASO10} + LUs	2147.8	2170.1
	CDDi _{Oct10} + LUs	2148.7	2171.1
	T _{min-Oct} + LUs	2148.0	2170.7
	RD _(Sep.1–Oct.31) + LUs	2153.1	2175.4
	GDR _(Sep.1–Oct.31) + LUs	2154.3	2176.7

have on variation in autumn phenology. In addition, all models included onset or peak date of leaf unfolding as a significant predictor, indicating the important relationship between spring and autumn phenology. The models suggested that one day earlier in onset or peak of leaf unfolding lead to about $0.2\text{--}0.3 \pm 0.06$ days earlier for all autumnal transition dates of leaf coloration and leaf drop of trees during 2012 and 2014.

The best models based on 22 years of phenological observations at Harvard Forest (dataset 2) (Table 2 and S5) suggested that timing of leaf coloration and leaf drop of all species were significantly affected by temperature in autumn, precipitation in spring and summer, drought-stress in summer and autumn, heavy rainfall in autumn and summer heat stress. Overall, warming temperatures in autumn and more drought-stress in summer and autumn delayed leaf coloration and leaf drop, while more rainfall in the spring and more heavy rainy days in autumn lead to earlier leaf coloration and leaf drop. Specifically, each phenological transition date (cf. Fig. S1) was affected by chilling over the period, one to two months prior to the particular phenological event date (Table 2). Onset of leaf coloration was affected by Cold Degree Day (CDD) in August, but the peak dates of leaf coloration were affected by CDD in both August and September, while end of leaf coloration was affected by CDD in September and minimum temperature in October (T_{min-Oct}). For leaf drop, onset and peak, dates were affected by CDD in both August and September, but the end of leaf drop was affected only by CDD in September. In addition, significant positive correlations between spring and autumn phenology were found in models of leaf coloration transition dates across all species. One day earlier for end of leaf unfolding lead to about 0.1 ± 0.02 days earlier for the three

Table 2

Unstandardized coefficients of fixed variables from the best linear mixed effects models of autumn phenology for 12 deciduous tree species at Harvard Forest (1993–2014). For variable names refer to Table S3. CDD: cold degree day; RD: rainy day; GDR: growing season drought; $T_{\min}$: monthly minimum temperature. Subscript in each variable indicates the time period for each variable or the base temperature in calculations. LUE is leaf unfolding end date.

Phenophase	Predictor	Coefficient	SE	p-value
leaf coloration onset date	CDD _{iAug20}	−0.055	0.005	< 0.001
	RD _(May.1–Jun.30)	−0.258	0.067	< 0.001
	GDR _(Sep.1–Oct.31)	0.183	0.056	< 0.001
	LUE	0.070	0.031	0.011
leaf coloration peak date	CDD _{iAug20}	−0.028	0.005	< 0.001
	CDD _{Sep20}	−0.043	0.006	< 0.001
	RD _(May.1–Jun.30)	−0.114	0.051	0.013
	LUE	0.104	0.022	< 0.001
leaf coloration end date	CDD _{Sep20}	−0.076	0.005	< 0.001
	$T_{\min}$ -Oct	0.369	0.126	< 0.001
	GDR _(Jul.1–Aug.31)	0.095	0.041	0.011
	LUE	0.126	0.022	< 0.001
leaf drop onset date	CDD _{iAug20}	−0.036	0.006	< 0.001
	CDD _{Sep20}	−0.031	0.008	< 0.001
	RD _(May.1–Jun.30)	−0.173	0.072	0.008
	RD _(Jul.1–Aug.31)	0.331	0.071	< 0.001
leaf drop peak date	CDD _{iAug20}	−0.019	0.005	< 0.001
	CDD _{Sep20}	−0.059	0.007	< 0.001
	RD _(May.1–Jun.30)	−0.194	0.065	0.002
	RD _(Jul.1–Aug.31)	0.309	0.057	< 0.001
leaf drop end date	CDD _{Sep20}	−0.077	0.005	< 0.001
	RD _(Jul.1–Aug.31)	0.334	0.062	< 0.001
	GDR _(Jul.1–Aug.31)	0.165	0.037	< 0.001

autumnal transition dates of leaf coloration of trees at Harvard Forest over 1993–2014 (Table 2). In order to compare the relative contribution from selected important factors in explaining phenological variation, we calculated standardized coefficients for fixed variables in the best models (Table S4). Results suggested that cold degree day had stronger effects (0.23–0.28) on autumn phenology than other climate/weather variables (0.05–0.10) and spring phenology (0.05–0.11).

3.2. Species-specific phenological responses to weather stressors

While autumn phenology for the 12 species showed the same responses to the effects of chilling in autumn, random slopes of the climate/weather factors selected in the models suggested different sensitivities (i.e. the magnitude of the coefficients of these factors) of autumn phenology among the 12 species in responses to changes in drought-stress, heat-stress, and rainfall over the growing seasons (Fig. 2). Overall, the timing of leaf coloration had different responses among species to spring rainfall (RD_(May.1–Jun.30)), summer and autumn drought stress (GDR_(Jul.1–Aug.31) and GDR_(Sep.1–Oct.31)), and heavy rainfall in autumn (ECA_(Sep.1–Oct.31)). The timing of leaf drop processes had different responses among species to spring rainfall, plus drought and heavy rainfall in autumn. Species with earlier autumn phenologies, including white ash, maples, and birches, had higher sensitivities to drought-stress in the summer (GDR_(Jul.1–Aug.31)) and autumn (GDR_(Sep.1–Oct.31)), than those species with later autumn phenology (i.e. oaks and beech) (Fig. 2). Among the 12 species examined, the autumn phenology of paper birch had higher sensitivities to climate/weather variables, including rainfall in spring (RD_(May.1–Jun.30)), drought in summer and autumn (GDR_(Jul.1–Aug.31) and GDR_(Sep.1–Oct.31)), and heavy rainfall in autumn (ECA_(Sep.1–Oct.31)), than any of the other species (16 out of 21 variables across 6 models, Fig. 2).

Regarding the timing of onset and peak of leaf coloration, spring rainfall (RD_(May.1–Jun.30)) lead to earlier leaf coloration onset and peak dates of all 12 species (Fig. 2). However, heavy rainfall in autumn (ECA_(Sep.1–Oct.31)) delayed leaf coloration onset dates of six species (yellow birch, grey birch, striped maple, black oak, red oak, and American beech) and peak dates of four of the species (striped maple,

black oak, red oak, and American beech). While drought-stress in summer and autumn (GDR_(Jul.1–Aug.31) and GDR_(Sep.1–Oct.31)) delayed leaf coloration onset of six and eleven species and leaf coloration peak dates of eight and nine species, summer drought-stress (GDR_(Jul.1–Aug.31)) advanced leaf coloration onset dates of six species (yellow birch, grey birch, striped maple, black oak, red oak, and American beech) and leaf coloration peak dates of four of the 12 species (striped maple, black oak, red oak, and American beech) (Fig. 2). Autumn drought-stress (GDR_(Sep.1–Oct.31)) advanced leaf coloration onset dates of American beech and leaf coloration peak dates of three of the species (black oak, red oak, and American beech). In addition, higher minimum temperature in October ($T_{\min}$ -Oct) lead to later leaf coloration end dates except in two species (white ash and paper birch). More summer heat-stress (HD₃₅) lead to earlier leaf coloration end dates of most species except three species (black oak, red oak, and American beech) (Fig. 2). More drought-stress in summer and autumn (GDR_(Jul.1–Aug.31) and GDR_(Sep.1–Oct.31)) delayed leaf coloration end dates of most species, but more summer drought advanced leaf coloration end dates for red oak, while more autumn drought advanced leaf coloration end dates of striped maple, black oak, red oak, and American beech (Fig. 2). In terms of the timing of leaf drop, more spring rainfall and heavy rainfall in autumn lead to earlier leaf drop, and more autumn drought-stress delayed leaf drop of most species. However, the three transition dates associated with leaf drop for four species (white oak, black oak, red oak, and American beech) were advanced by autumn drought-stress and delayed by heavy rainfall in autumn, in contrast to the other 8 species (Fig. 2).

3.3. Phenological variation among individual trees, species and sites

The best models for observations at Harvard Forest over 22-years (dataset 2) showed that standard deviations in onset, peak and end dates of leaf coloration among all 12 species were respectively 4.6, 6.3, and 5.9 days, and about 7.0, 5.8, and 3.9 days respectively among individuals within species. For the leaf drop, the standard deviations in onset, peak and end dates among 12 species were 4.8, 5.9, and 7.0 days, and among individuals within species they were 5.4, 4.4, and 4.2 days respectively (Table S5). Additionally, the best models applied to 3-year observations at Connecticut and Harvard Forest (dataset 1) showed that standard deviations in onset, peak and end dates of leaf coloration, that were not explained by climate/weather factors in the models, were respectively 9.0, 9.6, and 9.9 days among all eight species across all sites, and about 4.6, 4.5, and 4.8 days respectively among sites within species. For the leaf drop, the standard deviations in onset, peak and end dates among eight species across all sites were 9.5, 10.6, and 11.7 days, and among sites within species they were 5.9, 5.3, and 5.2 days respectively. By calculating the marginal and conditional r^2 of our best models for the observations at Harvard Forest over 22-years (Table S6), we found that the fixed variables (climate/weather) in the models explained much less variation (year to year) in phenological dates than what the random effects explained (variation among species and individuals). In the model evaluations, comparisons between predicted and observed dates of six transition dates showed that our model prediction uncertainties were about 5–7 days, and r^2 were about 0.7 (Fig. S3). We also found that predictions of phenology had poorer performances ($r^2 = 0.07$ – 0.28 , RMSE = 9.7–12.2) in model evaluations when random effects at individual or species levels in the model were not included.

3.4. Predicted phenological shifts under future climate change

After model selection and validation on the Harvard Forest models, all transition dates of leaf coloration and leaf drop were predicted for all 52 individual trees at Harvard Forest using the best models, based on future climate change and predicted leaf unfolding end dates (Table S7) during 2015 and 2099. To summarize the phenology changes of each

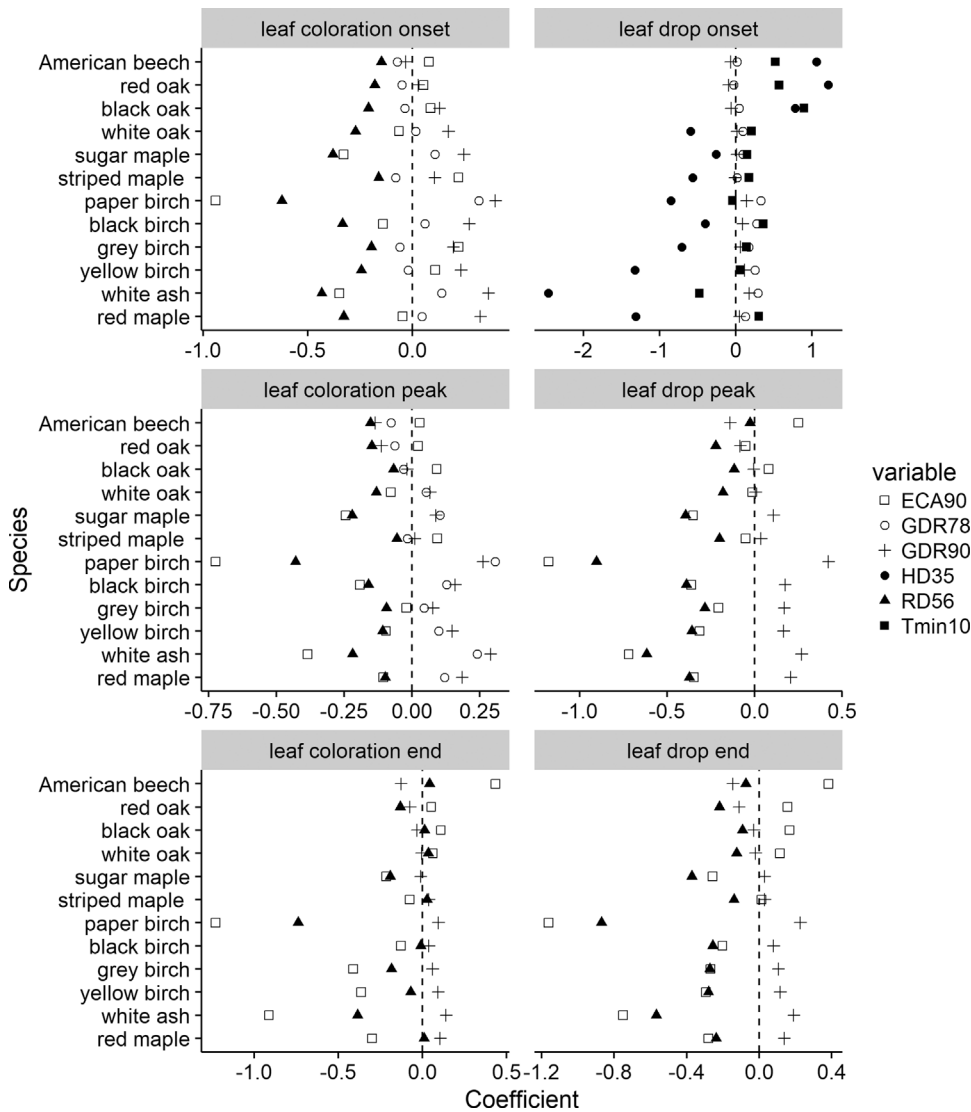


Fig. 2. Unstandardized coefficient values of random, species-specific slopes for fixed climate/weather variables in the best models for autumn phenology for 12 deciduous tree species at Harvard Forest (1993–2014). Y axis displays the 12 tree species. X axis displays coefficient values of the predictors. Each panel represent one phenological transition date (cf. Fig. 1S). Predictors are displayed by different symbols. RD56 ($\blacktriangle$): RD_(May.1–Jun.30); GDR78 ($\circ$): GDR_(Jul.1–Aug.31); GDR90 ($+$): GDR_(Sep.1–Oct.31); ECA90 ($\square$): ECA_(Sep.1–Oct.31); Tmin10 ($\blacksquare$): T_{min-Oct}; HD35 ($\bullet$): HD₃₅.

species, we calculated the change in days of each phenological transition date during 1993 and 2009 for each individual tree (Fig. 3). We found that 12 species showed different predicted trends of changes (earlier or later) in the phenological dates in the future. For the onset dates of leaf coloration, striped maple and American beech are projected to be 3.2–4.8 days earlier, while other species are projected to be 1.2–14.2 days later by the end of this century. For the peak dates of leaf coloration, striped maple and American beech are projected to be 0.3–4.5 days earlier, while other species will likely be 2.1–16.4 days later by the end of this century (Fig. 3). While striped maple, yellow birch, and American beech are projected to have leaf coloration end dates 14.4–30.5 days earlier by the end of this century, red maple, paper birch, red oak, and black oak will likely be 8.9–36.3 days later. The other five species, sugar maple, black birch, grey birch, white ash and white oak, showed smaller predicted changes (5.3 days earlier to 2.6 days later) in the end of leaf coloration compared to current years (Fig. 3). For the changes in phenology transition dates of leaf drop, all but one species were predicted to be later. By the end of this century, the onset of leaf drop for 11 of the 12 species are predicted to be 1.3–25.5 days later, while the changes of American beech will vary among individual trees (from 2.6 days earlier to 4.4 days later). For the other 11 species, peak and end dates of leaf drop were predicted to be delayed between 2.3–26.8 and 3.4–23.8 days respectively by the end of this century, while American beech was projected to have various

changes among individuals (5.2 days earlier to 2.2 days later for leaf drop peak date and 0.8–8.8 days earlier for leaf drop end date) (Fig. 3).

4. Discussion

4.1. Diverse phenological responses to weather stressors among tree species

This study identified important climate/weather factors affecting autumn phenology of a suite of deciduous tree species in northeastern USA forest systems, and provided insights into autumn phenological mechanisms at the species and individual levels, as well as local site effects. Our models suggested that while timing of leaf coloration and leaf drop of deciduous tree species respond to heat-stress, drought-stress and rainfall across the whole growing season, different species have different phenological responses to these factors. These differences could be related to species-specific physiological requirements and adaptations to environmental variation. For example, species that are less drought tolerant (e.g. white ash, maples and birches) (Pääkkönen et al., 1998; Prasad and Iverson, 2003) showed higher sensitivities to drought than species with greater drought tolerance (e.g. oaks and beech) (Abrams, 1990; Zolkos et al., 2015). In addition, they had opposite responses to drought-stress in summer and autumn, which delayed autumn phenology in ash, maples and birches and advanced autumn phenology in oaks and beech. One reason for this difference

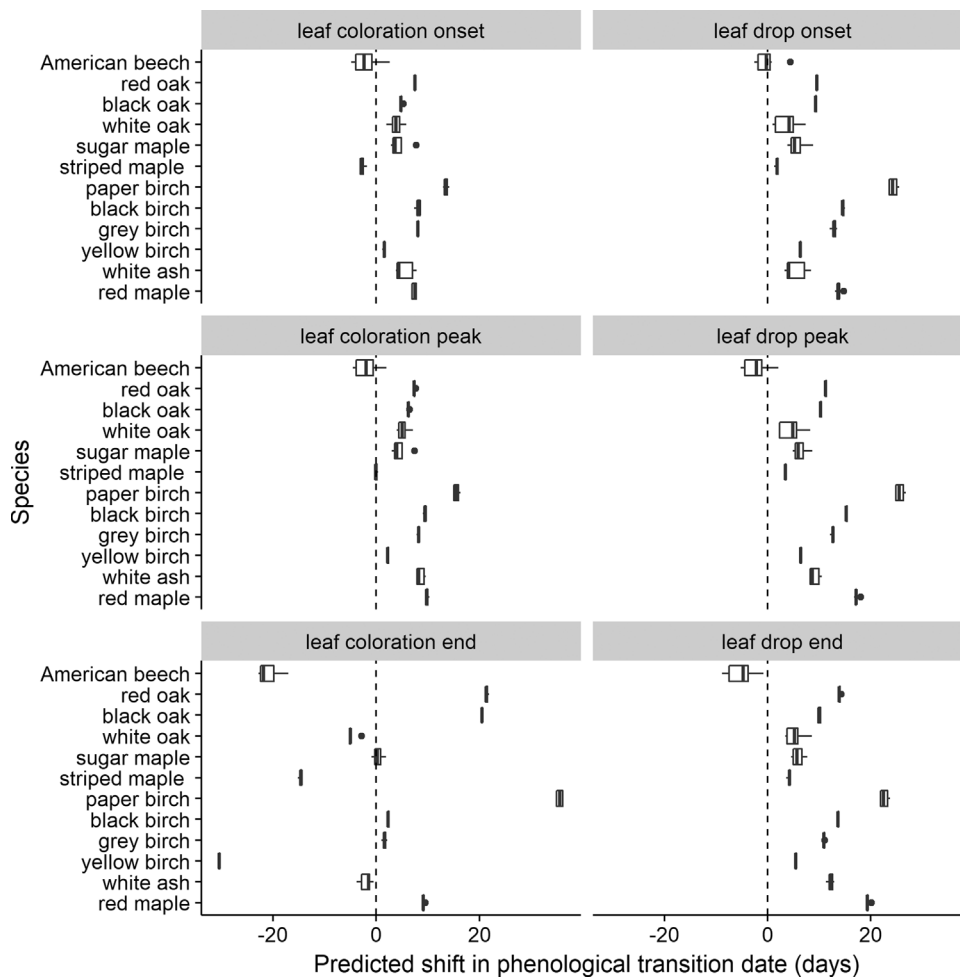


Fig. 3. Predicted changes in phenological transition dates (days) among 12 species between 1993 and 2099. Negative values indicate phenology dates are predicted to come earlier while positive values indicate later phenological transition dates by the end of this century. Each boxplot shows variation of change in phenology dates among individuals within each species from the minimum, 25th, 50th, and 75th quantile, and maximum values.

may be molecular and physiological responses to moderate drought-stress by gene regulation on plant hormones and stress-shock proteins (Carvalho et al., 2014). Another explanation could be the heterogeneity among micro-environments in our forest study system. White ash, maples and birches prefer moister soil, while oaks and beech tend to tolerate drier soil condition (Prasad and Iverson, 2003). However, local variation in site conditions (e.g. generally wetter or drier microsites) may elicit different responses in different species under moderate or severe climatic drought conditions locally or regionally. Although oaks and beech are less sensitive to drought, they can avoid severe drought-stress by entering leaf senescence earlier, preventing loss of resources and nutrients by drought-induced leaf death (Hinckley et al., 1979). The diverse sensitivities to climate/weather conditions among species may be also related to characteristics of leaf traits, leaf longevity, costs/benefits associated with photosynthetic physiology vs. nutrient budgets, and stage of ecological succession (pioneer species versus climax species) (Chabot and Hicks, 1982; Kikuzawa, 1995; Wright et al., 2004; Onoda et al., 2011; Kikuzawa et al., 2013). For example, oak and beech species have thicker leaves and greater leaf mass per area (LMA) than other species, so they tend to have longer leaf life span and lower sensitivities to drought than other species. Sensitivities of autumn phenology to environmental stress among tree species also reflect their adaptation strategies, since the timing of leaf senescence significantly relates to the benefit-cost strategy between photosynthesis and nutrient reallocation (Kikuzawa et al., 2013; Estiarte and Peñuelas, 2015). Further research based on long-term phenology observations with a larger sample size across more species over a larger spatial area, along with measurements on leaf traits and other characteristics (e.g. photosynthetic rate and successional stage) (Nagai et al., 2017; Nagai and

Nasahara, 2017), would benefit to improve our understanding of the resilience and vulnerability of ecosystem function and services to climate change.

4.2. Phenological variations in mixed-effects models

The advantage of nested mixed-effects models is that the random intercepts, varying at individual, species, or site levels, allowed us to investigate variation in phenology among individuals (Fig. S2), species or sites, that were not fully explained by climate/weather factors alone in the models. Our findings indicated that including the variation among individuals, species and sites could be critical in improving the accuracy of phenological predictions, rather than using averaged phenological dates for the species, or ignoring the individual or site variation effects. It is noteworthy that the variation among sites or individuals within species (Fig. S2) have been previously noted (Crawley and Akhteruzzaman, 1988; Ne'Eman, 1993; Delpierre et al., 2017), but have rarely been explicitly considered in previous phenological modeling studies (Kramer et al., 2008; Oddou-Muratorio and Davi, 2014). Our mixed-effects models provided quantitative phenological variations among species, individuals and/or locations from random effects, and the variations driven by climate/weather conditions from fixed effects, which suggested the variation in autumn phenology among species, individuals and sites were larger than year to year variation driven by changes in climate/weather variables. However, Dynamic Global Vegetation Models (DGVM) typically only apply plant functional types and temperature threshold to the phenology components (Sitch et al., 2008), which may cause biased prediction due to the lack of species-specific phenological responses and variations from site effects and

individual differences. Tree species-based dynamic models have been developed with species-specific parameters often for particular study sites or regions (Badeck et al., 2001; Delpierre et al., 2012), and have rarely been applied at large scale changes in vegetation (Koca et al., 2006; Hickler et al., 2012). Therefore, our results suggest that it is important to incorporate variability among individuals within species, species-specific phenological responses, and site heterogeneity in the ecosystem models (Kramer et al., 2008; Oddou-Muratorio and Davi, 2014). The consistent difference of phenology among individual trees within species and sites could be caused by health condition of the individual tree (e.g. pests, pathogens or other stresses), local hydrological conditions due to ontogeny and micro-environment (e.g. soil texture and nutrients) in the particular location in the forest, or genotypic effects (Huber and Gillespie, 1992; He et al., 2005; Hwang et al., 2014; Delpierre et al., 2017; Cole and Sheldon, 2017). Thus, we encourage further research and experiments to investigate the factors that affect individual phenological variations within species.

4.3. Phenological shifts driven by future weather stressors

Based on the climate change projections in the future, later autumn phenology was predicted on average, with considerably variation in magnitudes of changes among species, from no more than 1 day to more than 20 days, and advanced autumn phenology varying from no more than 1 day to 30 days were also predicted. These large variations in future projected responses reflect the species-specific sensitivities to the change in climate/weather factors. For example, paper birch with the highest sensitivities to drought-stress, heat-stress and heavy rainfall, always showed the largest predicted changes in the future (14.2–36.3 days later across all event dates of leaf coloration and leaf drop) in response to projected climate change. Our predictions also suggested a reduced length of the leaf senescence process in the future for at least seven of twelve species. This change reflects more heat-stress predicted in the future (more than 10 HD₃₅ by 2099 compared to 1 HD₃₅ in current years), especially towards the end of this century. Greater heat-stress tends to speed up the process of leaf coloration, while warm climates overall lead to later start of leaf coloration. Our models showed that summer heat-stress had the largest effect on the length of leaf coloration season. Each additional hot day (HD₃₅) reduced the length of leaf coloration by 4.2 days across our 12 species on average. In contrast, increasing one unit of chilling in autumn and summer drought reduced on average the length of the fall color season by only 0.02 and 0.1 days respectively, and while increasing one heavy rainy day in autumn tended to increase the season length by 0.9 days. Given more heat-stress predicted for future years, based on climate projection data for north-eastern USA (Abatzoglou and Brown, 2012), the length of leaf coloration season is predicted to be strongly reduced, by about 20–40 days. This may in turn have significant effects on community and ecosystem processes. For example, a shorter leaf coloration period may reduce the efficiency of nutrient resorption from leaves during leaf senescence, which could challenge plant nutrient economies and alters nutrient flows through the ecosystem (Estiarte and Peñuelas, 2015). Individual functioning of tree growth may be also affected by the inter-individual variation in autumn phenology (Delpierre et al., 2017). In addition, the economic impact of the fall foliage ecotourism industry may be influenced by shorter time periods of brilliant fall foliage.

Our study had the similar future predictions regarding autumn phenological shifts as some previous studies (Archetti et al., 2013; Keenan and Richardson, 2015). These included predicted delays autumn phenology, different timing shifts among species, altered leaf color duration, and reduced delays of autumn phenology driven by spring phenological shifts. The main difference was that our study also reported advanced leaf coloration end dates for five species, and advanced leaf coloration and leaf drop for American beech, as driven by higher summer heat-stresses. The other difference we found was that the different shifts in magnitudes among species were driven by the

species-specific sensitivities to climate/weather stressors in our models. Further observations with larger sample sizes over larger spatial extents on autumn phenology should be used to test our predictions and to build better models.

In our future prediction of leaf coloration dates, some anomalies were found in the timing of successive phenophases for five species (striped maple, yellow birch, white ash, white oak, and American beech) after year 2070, i.e. leaf coloration end dates were predicted to be earlier than leaf coloration onset dates. These results were caused by the strong negative effects from summer heat on leaf coloration end dates for these species. These results suggest that models that incorporate the covariance between phenophases may improve model performance and realism. We developed our models for each phenophase independently, since we had an underlying hypothesis regarding autumn phenology that each phenophase may be driven by different gene regulatory processes with respect to environmental variables (Wilczek et al., 2010). Phenophase-specific models allowed us to compare how different climate/weather variables affected each phenophase, which was one of our main goals. From our predictions, the strong effects from summer heat-stress on leaf coloration end date points to an important insight: that phenological responses to environmental stress may be phenophase-specific or more complex than we might have anticipated. We are aware of our model limitation that did not constrain phenological responses based on the prior phenophase (Archetti et al., 2013), but the size of our databases did not allow for more complex models that could also incorporate this constraint. In the further research with larger datasets, we plan to use multivariate regression or process-based models to include the dependence of phenophases, but this is beyond the capabilities of the study reported here.

4.4. Implications for improving phenological understanding

Compared to the best models based on the 3-year dataset, the 22-year Harvard Forest dataset models did not select spring phenology as an important variable in models explaining leaf drop phenology (Table 2). Important climate/weather variables including CDD, RD and GDR from different seasons were selected in the best models based on two datasets. The reason for these two differences is likely that the 3-year dataset had relatively little inter-annual variation in these variables compared to the 22-year dataset. This is likely reflected by the fact that we found more than one model with small differences in AIC and BIC (i.e. smaller than 5; Table 1). Our results suggest that the correlation between spring phenology and leaf coloration dates could be much stronger than the correlation between spring phenology and leaf drop dates based on long-term variation. This could be because leaf coloration is more related to end of leaf longevity and associated photosynthesis activities than is leaf drop during the growing season. Thus, the constraints from leaf structural characteristics on longevity and carbon sink limitation may have stronger effects on leaf coloration dates than leaf drop (Fu et al., 2014; Keenan and Richardson, 2015). This also points to the facts that long-term phenological datasets are critical in resolving those environmental factors that provide insight into the underlying mechanisms of autumn phenological change in plants.

Compared to the studies working on some of the same phenology dataset from Harvard Forest (Archetti et al., 2013; Keenan and Richardson, 2015), our study provides four unique perspectives in phenological modeling: the role of site, species and individual effects (hierarchically), a broader suite of potential explanatory variables (including known plant stressors), the effects of each of these explanatory variables on each autumn phenophase (based on the likelihood that each phenophase may respond differently to each climate/weather variable), and incorporating this information into predictions of how autumn phenology may respond to projected future climate change. Our models had a lower marginal r^2 than those of Archetti et al. (2013), but a higher conditional r^2 . However, it is not appropriate to directly

compare r^2 values between these two studies because Archetti et al. (2013) averaged individual phenology within each species prior to fitting the model for each species, which did not include inter-individual or inter-specific variations. The r^2 values from Archetti et al. (2013) represented the percentage of inter-annual phenological variation explained by the models without individual-level or species-level variability. The models in our study included not only inter-annual variation, but also inter-individual and inter-specific variation in autumn phenology. The r^2 from our models represented the percentage of all three types of variations mentioned above explained by the models, which lead to much smaller marginal r^2 . In terms of future predictions, the models from Archetti et al. (2013) provided one predicted value in one year to represent future autumn phenological shift for each species. Our models provided one predicted value in one year for each individual of each species in the dataset, which yields variation in predictions (i.e. uncertainty) for each species. Overall, each study provides unique contributions to autumn phenology modeling. Archetti et al. (2013) revealed the advantage using process-based model to simultaneously estimate five stages of leaf coloring and leaf drop at the species level. Our models demonstrate the advantages of incorporating inter-individual and inter-specific variation along with site effects to estimate autumn phenological timing at the individual level.

Integrating the modeling approaches from both studies would improve our understanding of phenological responses and prediction of future shifts, though challenges exist in how to incorporate large inter-individual variation within species to develop reliable models for ecosystem model functioning. Compared to the relatively short process of spring phenology, autumn phenology involved much larger inter-individual and inter-specific variation. Phenological observations on only a few individuals using common observation protocols consequently limit our modeling capabilities, since this sample size will not be big enough to capture phenological variation within populations or species. Due to this limitation, even using an averaged value from 3 to 5 samples may lead to potential biases in phenology modeling. In fact, the high inter-individual variations in phenology within species imply that phenotypic (i.e. plastic and genotypic) variation in populations as these respond to environmental changes can be quite large (Kramer et al., 2008; Oddou-Muratorio and Davi, 2014). Incorporating the known inter-individual variation in phenology models will benefit generating more accurate predictions (along with the uncertainty thereof) in response to climate change. However, this requires more detailed phenology observations and a much larger sample size.

5. Conclusion

From this study, our understanding of the complex mechanisms effecting the autumn phenology of deciduous tree species is significantly improved. Our models suggested that compared to chill effects, changes of climate/weather variables including drought, heat and precipitation, and spring phenology had smaller influences on autumn phenology, but the influences were still strong that cannot be overlooked in estimating phenological changes. Additional environmental factors beyond the standard variables of chill or frost days and spring phenology should be included in predictive models of fall phenology. Clearly extreme weather events (e.g. drought, heat and heavy rain), should be taken into account in explaining or predicting the timing of leaf coloration and leaf drop of deciduous trees, as well as site and individual effects. While projected climate change will likely bring increased intensity and frequency of extreme weather events (e.g. drought, heat and heavy rain) (Garcia et al., 2014), as well as significant changes of spring phenology (Cleland et al., 2007; Allen et al., 2014; Xie et al., 2015a), the impact on autumn phenology will likely be more complicated than previously thought. Autumnal phenological shifts of deciduous tree species are projected to be more diverse than expected due to species-specific phenological sensitivities to a range of environmental factors, individual and site effects, and spring

phenological responses (Fu et al., 2014; Keenan and Richardson, 2015). Our results reinforce the need for phenology observations on more species and sites, with greater replication over greater spatial-temporal scales. Citizen science observation networks (Denny et al., 2014) and near-surface time-lapse camera monitoring networks (Inoue et al., 2014; Nasahara and Nagai, 2015; Wingate et al., 2015; Brown et al., 2016; Kosmala et al., 2016; Moore et al., 2016) provide one way of achieving these goals. Controlled physiological experiments may also be necessary to more fully understand the physiological as well as molecular genetic mechanisms behind autumn phenology patterns and processes. Our study also provides insights to the study of forest senescence and dormancy along with information of species composition in a large spatial scale. These efforts can help inform us how to predict autumn phenology of deciduous trees in response to climate change now and in the future, as well as predict the future ecological and economic consequences thereof.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2017.12.259>

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